Development of habitat suitability indices and bioenergetics models for Arctic grayling (*Thymallus arcticus*)

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DEVELOPMENT OF A HABITAT SUITABILITY INDICES AND BIOENERGETICS MODELS FOR ARCTIC GRAYLING (*Thymallus arcticus*)

by

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TABLE OF CONTENTS

TABLE OF CONTENTS iii
ABSTRACT v
RÉSUMÉ v
1. INTRODUCTION 1
2. GENERAL MODEL APPLICABILITY 2
2.1. SPECIES DISTRIBUTION 2
2.2. LIFE HISTORY STAGES 3
2.3. BIOLOGICALLY SIGNIFICANT PERIODS 3
2.3.1. Spawning 3
2.3.2. YOY 3
2.3.3. Juveniles and Adults 4
2.3.4. Migrations and Overwintering 4
3. HABITAT SUITABILITY INDEX 5
3.1. OVERVIEW 5
3.2. HABITAT VARIABLES 6
3.3. OBTAINING DATA 7
3.4. CALCULATING THE HSI 8
3.5. HSI CURVES FOR SPECIFIC VARIABLES 10
3.5.1. Turbidity 10
3.5.1.1. All Life Stages *10*
3.5.2. Dissolved Oxygen 11
3.5.2.1. All Life Stages *11*
3.5.3. Water Temperature 12
3.5.3.1. All Life Stages *12*
3.5.4. Water Velocity 13
3.5.4.1. Spawning *14*
3.5.4.2. YOY *14*
3.5.4.3. Juveniles *15*
3.5.4.4. Adults *16*
3.5.5. Depth 17
3.5.5.1. Spawning *17*
3.5.5.2. YOY *18*
3.5.5.3. Juveniles *19*
3.5.5.4. Adults *20*
3.5.6. Substrate 21
3.5.6.1. Spawning *22*
3.5.6.2. YOY *22*
3.5.6.3. Juvenile *22*
3.5.6.4. Adult *22*

3.5.7. Cover 23
3.5.7.1. Spawning *24*
3.5.7.2. YOY *24*
3.5.7.3. Juvenile *24*
3.5.7.4. Adult *24*
3.5.8. Habitat Type 25
3.5.8.1. Spawning *26*
3.5.8.2. YOY *26*
3.5.8.3. Juvenile *26*
3.5.8.4. Adult *26*
3.6. DATA GAPS 27
3.7. COMPOSITE HSI 28
4. BIOENERGETICS 29
4.1. OVERVIEW 29
4.2. LIFE STAGE SPECIFIC MODELS 30
4.3. BASIC BIOENERGETICS MODEL 31
4.4. ENERGETIC COSTS 31
4.5. ENERGETIC GAINS 33
4.6. OTHER VARIABLES 35
4.7. INPUT VARIABLES 39
4.8. OUTPUT 39
4.9. DRAWBACKS 40
5. DISCUSSION 41
5.1. HABITAT SUITABILITY INDEX MODELS 41
5.2. BIOENERGETICS MODEL 43
6. SUMMARY 44
7. LITERATURE CITED 45

ABSTRACT

Larocque, S.M., Hatry, C., and Enders, E.C. 2014. Development of habitat suitability indices and bioenergetics models for Arctic grayling (*Thymallus arcticus*). Can. Tech. Rep. Fish. Aquat. Sci. 3097: vi + 57 p.

Fish habitat models are often used as tools to evaluate habitat quality for aquatic organisms. Habitat suitability indices are a commonly used in habitat models, while others, such as bioenergetics models, are beginning to utilize them more frequently. Recent legislative changes to the Canadian Fisheries Act have led to a focus on the conservation of the sustainability and the ongoing productivity of Canada's commercial, recreational, and Aboriginal fisheries rather than the former protection of fish habitat. Whereas the methods to evaluate the quantity and quality of fish habitat based on habitat suitability indices are well established, new methods have to be developed to assess the ongoing productivity of fisheries. Here, we explore the use of bioenergetics habitat models to assess habitat quality using the net energetic gain (NEG) of fish. Furthermore, we relate the NEG to the productivity and investigate the predictive power of bioenergetics habitat modelling in regards to flow and climate changes. Using Arctic grayling (*Thymallus arcticus*), a well-documented species sensitive to changes in habitat quality, we developed habitat suitability indices and a bioenergetics habitat model. When appropriate, assumptions were documented at each stage throughout the development of the model.

RÉSUMÉ

Larocque, S.M., Hatry, C., and Enders, E.C. 2014. Development of habitat suitability indices and bioenergetics models for Arctic grayling (*Thymallus arcticus*). Can. Tech. Rep. Fish. Aquat. Sci. 3097: vi + 57 p.

Les modèles d'habitat du poisson sont souvent utilisés comme outils afin d'évaluer la qualité de l'habitat. Dans ces modèles, les indices de qualité de l'habitat (IQH) sont couramment utilisés. D'autres modèles, tel que les modèles bioénergétiques, commencent à les utiliser plus fréquemment. Les récents changements législatifs à la Loi sur les pêches du Canada mettent l'accent sur la durabilité et la productivité continue des pêches commerciales, récréatives et autochtones ; plutôt que la protection de l'habitat du poisson. Considérant que les méthodes d'évaluation de la quantité et de la qualité de l'habitat du poisson en fonction des IQH sont bien

établies, des nouvelles méthodes doivent être mises au point pour évaluer la productivité continue des pêches. Ici, nous explorons l'utilisation de modèle d'habitat bioénergétique pour évaluer la qualité de l'habitat en utilisant le gain énergétique net (GEN) du poisson. De plus, nous mettons en relation le GEN avec la productivité et évaluons la qualité des prédictions du modèle bioénergétique de l'habitat en ce qui concerne l'écoulement et les changements climatiques. En utilisant l'ombre arctique (*Thymallus arcticus*), une espèce sensible aux changements de qualité de l'habitat, nous avons développé des IQH et un modèle bioénergétique. Les hypothèses ont été documentées à chacune des étapes tout au long du développement du modèle.

1. INTRODUCTION

Fish habitat models are an important tool for river management as they can quantitatively evaluate habitat quality for aquatic organisms. Thus, fish habitat models are often used for purposes such as to: (1) determine habitat loss and the amount of compensation required; (2) monitor fish habitat at contaminated sites; (3) evaluate habitat restoration projects; or (4) establish Instream Flow Needs (IFN) requirements. Fish habitat models may also be used in future studies to complement population based assessment methods. Researchers have identified fish productivity (numbers or biomass) as one of the most important tenets of maintaining the productive capacity of fish habitat (Jones et al. 1996; Randall and Minns 2000) and have suggested the need for integrating population responses to habitat characteristics (Minns et al. 2011). Fish habitat models can also be used in this context.

A variety of different fish habitat models exist (see de Kerckhove et al. 2008). One of the most commonly used models for quantifying changes to fish habitat are based on Habitat Suitability Indices (HSIs; de Kerckhove et al. 2008). HSIs incorporate the selection and preferences of different habitat variables to determine the most optimal habitat for the selected fish species. HSIs typically rely on the use of physical habitat variables (velocity, depth, and substrate), which are important for lotic environments where water flow can be variable (Bovee 1986) but are also used for lakes and marine coastal areas (Cook and Solomon 1987, Brown et al. 2000, respectively). In the absence of field data, HSI curves are often obtained from other regions or by expert opinion and may not be applicable to Canadian environments and fish populations. To ensure a consistent approach to the evaluation of habitat restoration projects across the country, Fisheries and Oceans Canada's Fisheries Protection Program needs Canadian-specific HSI curves for key fish species.

Another type of fish habitat model is the bioenergetics model, which is based on a mechanistic approach. Bioenergetics models are becoming more frequent in the literature for quantifying fish habitat (Hughes and Dill 1990; Hughes 1998; Jenkins and Keeley 2010). They incorporate biological variables as well as physical variables into the model. Specifically, they include food availability, which the physical habitat model omits. For this reason, bioenergetics models can

potentially improve the ability to quantify habitat quality compared to HSIs (Rosenfeld et al. 2005).

Using both HSI and bioenergetics models, we created fish habitat models, from the literature, specific to Canadian environments. In particular, the models focused on Arctic grayling (*Thymallus arcticus*). We selected this species because its sensitivity to contaminants, turbidity, temperature, and flow changes and requirements for unfragmented habitat to move between various habitat types (Stewart et al. 2007a). As such, Arctic grayling are responsive to changes in habitat quality. Furthermore, biological information exists for Arctic grayling from which the habitat models could be created.

2. GENERAL MODEL APPLICABILITY

Habitat models for any species are only applicable under certain circumstances. Different life stages (e.g., juvenile, adult), and Biological Significant Periods (BSPs; e.g., breeding, migrating) can have different habitat preferences. In our case, the HSI and bioenergetics models were built from information pertaining to the Arctic grayling (*Thymallus arcticus*). As such, the models are applicable to areas within the species natural distribution (this does not include stocked populations), to the specified life stage, and only during the BSPs relevant to the specified life stage. It is important to note that there are differences among riverine and adfluvial Arctic grayling, and we focused on the more commonly occurring riverine fish.

2.1. SPECIES DISTRIBUTION

Arctic grayling reside in northern freshwater drainages (Scott and Crossman 1973). In North America, Arctic grayling occur throughout Alaska and the Northwest and Yukon territories, as well as the Kitikmeot and Kivalliq regions of Nunavut (excluding Arctic islands); in northern areas of Manitoba (south to the Owl River), Saskatchewan (as far south as Reindeer Lake, but absent from much of the Churchill River), Alberta (south to central Alberta), and British Columbia (from the Peace and Stikine Rivers north) (Scott and Crossman 1973; Sawatzky et al. 2007; Stewart et al. 2007a). Arctic grayling distribution conforms closely with the following freshwater ecoregions (or watersheds): Yukon, Lower Mackenzie, Upper Mackenzie, North Arctic and East Arctic, as well as northern parts of North Pacific coastal (Abell et al. 2008).

2.2. LIFE HISTORY STAGES

The Arctic grayling life cycle was divided into four categories to better illustrate each life stage's specific habitat requirements. Models specify which life stage they are applicable to. Life stages were divided as described in Stewart et al. (2007a):

- Spawning – The period which adult grayling spawn and the eggs mature, hatch, and emerge from the substrate (a sensitive period for both the adults and eggs).
- Young-of-year (YOY) – The period in which larvae and fry are less than age 1 (age 0 until December 31 of the year they are hatched).
- Juvenile - Sexually immature fish older than age 1.
- Adult - Fish that have attained sexual maturity.

2.3. BIOLOGICALLY SIGNIFICANT PERIODS

The Biological Significant Periods (BSPs) of Arctic grayling are illustrated in Figure 2.1. The BSPs have a wide range to encompass all possible times in which a BSP can occur over the species' geographical range, although the actual duration of a BSP may be significantly shorter (e.g., possible spawning times ranges 3.5 months but spawning only occurs for a few weeks). The BSPs are described in detail below.

2.3.1. Spawning

Spawning of Arctic grayling can occur anytime from April to early July but typically from mid May to mid June (Scott and Crossman 1973; Northcote 1995; Stewart et al. 2007a). Spawning generally begins after ice break up in streams and when water temperatures reach a minimum of 4 °C (Scott and Crossman 1973; Tack 1980; Northcote 1995). The actual spawning period only lasts 2-3 weeks (Ford et al. 1995).

2.3.2. YOY

After spawning occurs and eggs mature, fry (YOY) emerge and begin feeding approximately one month after spawning (Scott and Crossman 1973). Therefore, starting as early as May, although more typically by late May (Tripp and McCart 1974, Craig and Poulin 1975, Katopodis et al. 1978, Chang-Kue and Cameron 1980 cited in Stewart et al. 2007a) or late June (Ford et al. 1995;

Stewart et al. 1982 cited in Northcote 1995), YOY emerge and reside in streams until they migrate to overwintering sites.

2.3.3. Juveniles and Adults

Juveniles and adults are present year round. When not migrating, overwintering, or in the case of adults, spawning, juveniles and adults are present in streams and rivers during the summer to feed (Evans et al. 2002; Stewart et al. 2007a). Thus, summer feeding in adults and juveniles will occur from as early as mid April, but more typically June, until they migrate to overwintering grounds.

2.3.4. Migrations and Overwintering

Overwintering migration can start in early summer (approximately August) up until December (Stein et al. 1973a, Pearse 1974, Porter et al. 1974, Netsch 1975, Armstrong 1986, Stanislawski 1997 cited in Stewart et al. 2007a) but usually occurs in September (Hubert et al. 1985; Northcote 1995; Armstrong 1986 cited in Stewart et al. 2007a). Arctic grayling migrate from streams and rivers to overwinter in large rivers (in deep pools) or lakes (Scott and Crossman 1973; Ford et al. 1995; Evans et al. 2002; Stewart et al. 2007a). Overwintering typically occurs from September until April (Hubert et al. 1985; Stewart et al. 2007a). The spring migration of adults into smaller streams occurs just prior to the spawn (as early as late March) and typically from mid-April up until May or mid-May (Hubert et al. 1985). After the adults, the juvenile spring migration occurs to streams and rivers in which they begin to feed instead of spawn. Adults may migrate from spawning streams to feed in larger streams in mid to late June (Chang-Kue and Cameron 1980 cited in Evans et al. 2002).

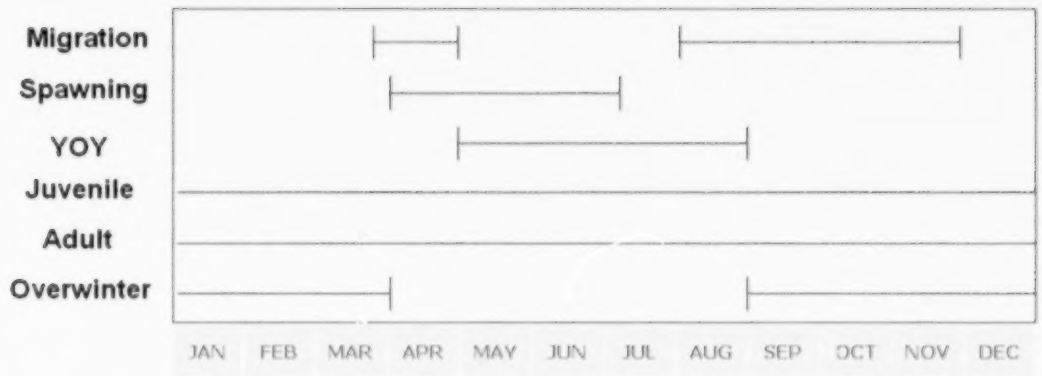

Figure 2.1. Approximate timing and duration of annual Biologically Significant Periods in the life cycle of Arctic grayling (*Thymallus arcticus*).

3. HABITAT SUITABILITY INDEX

3.1. OVERVIEW

HSIs are one of the most commonly used tools to objectively quantify and evaluate habitat quality of a selected species (Ahmadi-Nedushan et al. 2006; de Kerckhove et al. 2008). HSIs use physical habitat variables to determine the ability of a habitat to support a species by quantifying the species habitat requirements. Although actual habitat requirements depend on fitness consequences, habitat requirements are often inferred by a species preference or selection for particular habitat conditions (Rosenfeld 2003). The ability of the habitat to support a species or, in other words, the habitat suitability for the given species is described in an index that ranges between 0 (does not meet the species' preferences) and 1 (fully meets the species' preferences). Generally, separate suitability indices are created for different habitat variables (e.g., depth, velocity, and substrate) that have a direct or indirect effect on the species' fitness. However, as physical habitat is dependent on more than one variable, the suitability indices from key habitat variables need to be combined to form a composite HSI (Ahmadi-Nedushan et al. 2006). It is the composite HSI, which produces one measure of the overall habitat suitability that is used to predict the ability of a study area or habitat to support a given species.

A series of steps are involved with the development of HSIs: 1) Determining which habitat variables to include; 2) collecting the data on the species habitat preferences for each variable; 3) creating suitability indices for each habitat variable; and 4) combining the indices to create a

composite HSI. The HSI for Arctic grayling was developed using the above steps, which are discussed below. It is important to note that many assumptions and potential bias can occur in any of the steps to create an HSI, as well as when validating and applying the HSI. These assumptions and biases are mentioned as they occur.

3.2. HABITAT VARIABLES

Determining the habitat variables to be used in the HSI is important and should relate to the ability of the selected species to inhabit the environment. Thus, ideal environmental variables, if modified, would be expected to affect the capacity of the habitat to support the selected species by altering the species' fitness consequences (USFWS 1981; Rosenfeld 2003). These variables must be easily measureable but also reflect the spatial scale of the study. Most HSIs are at a local or microhabitat scale (e.g., within a stream) and use local habitat variables (e.g., width, depth, substrate, cover, flow type, bank side vegetation), however, as the scale increases, macrohabitat or catchment-scale variables (e.g., altitude, flow, stream order, geology, primary productivity indices) should be considered as well (Armstrong et al. 2003; Ahmadi-Nedushan et al. 2006; de Kerckhove et al. 2008). Also, using habitat variables from different scales may improve the transferability of models, as those developed for one localized stream rarely work in another stream type or region (Armstrong et al. 2003).

The most commonly used physical variables for characterizing microhabitat in stream fishes are velocity, depth, substrate, and cover (Bovee, 1986; Vadas and Orth 2001; Rosenfeld 2003; Ahmadi-Nedushan et al. 2006). At the microhabitat scale, fish tend to associate with certain velocities, depths, substrates, and cover, which aggregate together into a habitat preference. These four physical variables are particularly popular with HSIs as they are often involved in predicting habitat quality in stream fish using hydraulic models such as the Physical Habitat Simulation System (PHABSIM; Bovee 1986). However, other variables can also be important in predicting habitat selection, and may override selection for specific depths and velocities. For example, other variables that could affect stream fish survival and fitness are turbidity (e.g., by limiting vision and foraging abilities), dissolved oxygen (DO), water temperature (important for ectotherms), habitat type (mesohabitat that is typified by slope, channel shape and structure, may be of more importance than specific microhabitat characteristics – e.g., pool, riffle, run), and

competition (via introduced species or natural dominant competitors). By using only depth, velocity, substrate, and cover for an HSI, the HSI may not discern that murky, warm waters at an optimal depth and velocity may not be suitable for a visual predator, such as Arctic grayling that inhabits clear, cold streams. Taking into consideration that some variables are more difficult to measure when baseline information is minimal (e.g., presence of competitors), we focused on using turbidity, DO, temperature, water velocity, water depth, substrate, cover, and habitat type in our HSI.

Other variables, aside from microhabitat variables, may also be considered in HSIs. Ensuring habitat connectivity between all the life stages and home range is important for populations to persist and HSIs to be reliable (Roloff and Kernohan 1999). Arctic grayling need to successfully migrate annually to fulfill their life stage requirements (e.g., overwinter, spawn). A more reliable HSI may be developed by ensuring successful migration variables such as barriers to migration and migration distances are included. Culverts or other potential barriers (e.g., dams) can block fish passage from one site to other feeding, spawning, and overwintering sites, reducing successful completion of life stage requirements. Also, available spawning and overwintering spots need to be within migrating distance (up to 320 km; Evans et al. 2002). Other variables that may be considered are those at the catchment-scale (e.g., geology, altitude, flow) and Armstrong et al. (2003) suggested these variables may improve HSI transferability between streams. At present, these proposed variables were not included in the Arctic grayling HSI yet but may be considered later.

Assumption:

- The habitat variables used in the HSI are drivers of population abundance and have an effect on species' survival.

3.3. OBTAINING DATA

According to Bovee (1986), there are three categories to generate the criteria for HSI curves. Category I indices are derived from life history studies in the literature and or expert opinion. Category II indices are derived from data collected in the field and based on habitat conditions where the species occurs, yet not their absence. Category III indices are derived from a combination of species occurrence habitat data and additional information on the available

habitat within the sampling reaches (where the species does not occur). However, HSIs derived from field data in one river may not accurately portray habitat quality for another river; the HSIs may be less transferable when built upon such specific data (Groshens and Orth 1993; Guay et al. 2003). As the HSI for Arctic grayling is supposed to apply to its entire geographic range, specifically within Canada, using river specific habitat use data would be labour intensive and may not be generalized enough to transfer across watersheds. Thus, to more accurately determine Arctic grayling habitat use we compiled data derived from the literature in a database to create a category I HSI.

Potential bias:

- Using data from different Arctic grayling populations. All information collected focused on the naturally occurring northern populations of Arctic grayling, which occur in Alaska and northern parts of Canada.
- Unavailable data sources. Although there were many reviews on Arctic grayling life histor (e.g., Hubert et al. 1985, Evans et al. 2002, Stewart et al. 2007a), the primary source information (which the review papers were citing) could not always be obtained. Thus, the database mostly contained "summary" information about certain habitat characteristics from the reviews instead of "raw" data from the primary sources. Using summarized data from compiled sources in a review can skew the actual preferences of Arctic grayling by reducing the number of data points that can be obtained. Alternatively, the skew can be amplified by having two review papers give similar values from the same main sources. Thus, obtaining the main sources would improve the HSIs.

Assumption:

- The data obtained from the literature provides a complete overview of all habitats utilized by Arctic grayling within its northern range of North America.

3.4. CALCULATING THE HSI

Data was collected from the literature and compiled into a database and then incorporated into a suitability index. For continuous variables (e.g., depth, velocity, temperature), data in the literature mostly appeared in ranges (e.g., YOY inhabit streams at depths from 5-50 cm). All

ranges were divided into each respective low (e.g., 5 cm) and high range values (e.g., 50 cm). Outside of the broadest range indicated by the lowest of the low range values and highest of the high range values, habitat suitability was 0. The medians (most common value) of the low and high range values were deemed optimal (suitability = 1) as well as everything in between these values. Medians were calculated instead of means because less weight is given to extreme values when few values are available. For categorical variables (e.g., habitat type, substrate, cover), the frequency of each category appearing in the literature was calculated and suitability was determined by dividing the frequency of each category by the maximum frequency observed. Using the frequency in which these qualitative descriptions appeared in the literature should indicate the actual preference and reduce any bias. Lastly, variables with little data (e.g., turbidity, DO, temperature) used a combination of median range values and best judgement from details in specific references to create the HSI.

Potential bias:

- Heterogeneous data. A lot of data came in a variety of formats, such as ranges and means (without standard errors), or with different types of information, such as optimal temperature ranges and critical thermal maximums (CTMs). Some references were obscure and would only give the upper or lower limit to a range (i.e., > 0.5 m·s^{-1}). Some data varied between being descriptive or quantitative (i.e., clear or turbid waters instead of 5 Nephelometric Turbidity Units (NTU); shallow streams instead of 0-0.15 m depth). These varying formats made it difficult to discern quantitative preferences. A fuzzy-based approach is one way to handle heterogeneous data (Salski 1999; Ahmadi-Nedushan et al. 2006). Another method, which was employed, is to use a relatively consistent procedure to obtain the HSI and reduce any bias from subjectively combining different data formats. Biologically relevant types of data were used (e.g., we disregarded CTMs as fish would behaviourally avoid temperatures below the maximum), and ranges were used almost exclusively due to their prominence in the literature.

Assumption:

- The medians from the low and high range values captures the range of optimal habitat (i.e., Index = 1)

- Frequency data should indicate the proportion of the variable actually utilized. For example, a reference describes substrate to be "mostly gravel with some sand". Although both gravel and sand count towards the frequency data, it is assumed that sand will have a low suitability as it won't appear in the literature often, while gravel will appear more frequently and have a greater suitability.
- Descriptive interpretations were accurate. For example, if Arctic grayling prefer "below riffles", it was interpreted to be a "run", as that is the typical type of habitat found below a riffle in a stream (Burton Jr. and Pitt 2002).

3.5. HSI CURVES FOR SPECIFIC VARIABLES

3.5.1. Turbidity

There was not enough data or information in the literature for HSI curves of individual life stages for Arctic grayling. With the information available, it appeared that all life stages were equally sensitive to turbidity at all times of the year. Thus, the HSI curve applies to all life stages and for all BSPs (i.e., year round). The HSI curve for all life stages is described below as well as displayed in tabular and graphical formats (Figure 3.1).

3.5.1.1. All Life Stages

Arctic grayling prefer clear water streams and are not found in turbid waters (Scott and Crossman 1973; Reynolds et al.1989; Northcote 1993; Evans et al. 2002; Stewart et al. 2007a). In Alaska, Arctic grayling have been documented to spawn in turbid environments caused by spring freshet. However, this may not be as optimal as a clear stream given the visual nature of courtship with grayling (Lucas and Baras 2001; Jones et al. 2003a). An increase of 5 NTU in waters by anthropogenic activity with Arctic grayling is not recommended (Reynolds et al. 1989; Scannell 1988 cited in Stewart et al. 2007a). Thus, waters between 0 and 5 NTU are optimal habitat (Index = 1) for Arctic grayling. At 8 NTU, Arctic grayling are not seen as often indicating habitat is sub-optimal (Index = 0.6; Townsend 1987 cited in Northcote 1993). At 20 NTU, feeding was impaired in YOY, thus, affecting survival and habitat is considered poor (Index = 0.3; Scannell 1988 cited in Stewart et al. 2007a). At 30 NTU and greater, Arctic grayling are not found at all (Index = 0; Suchanek et al. 1984 cited in Stewart et al. 2007a).

Turbidity (NTU)	Suitability Index
0	1.0
5	1.0
8	0.6
20	0.3
30	0
> 30	0

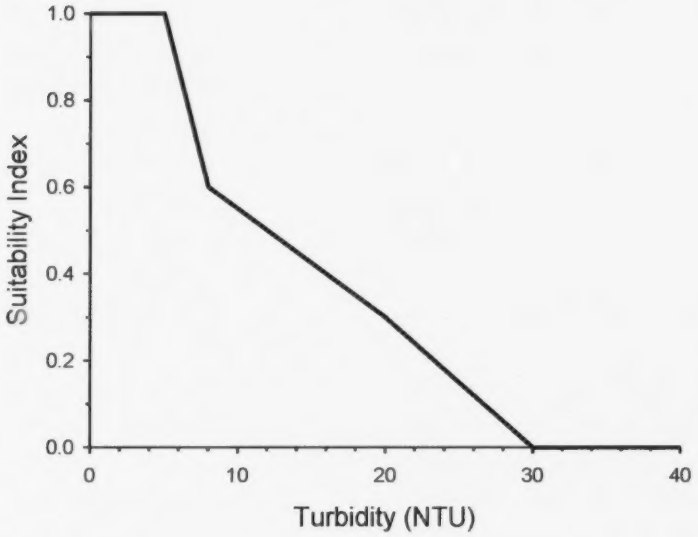

Figure 3.1. Habitat suitability curve of all life stages of Arctic grayling (*Thymallus arcticus*) at different turbidity levels (NTU).

3.5.2. Dissolved Oxygen

There was not enough data or information in the literature for HSI curves for each life stage of Arctic grayling. With the information available from laboratory experiments, it appeared that adults and YOY were equally sensitive to DO levels. Given that sufficient DO is a critical requirement for fish in any period of their life and at all times of the year, an HSI curve was developed that is suitable for all life stages and BSPs. The HSI curve for all life stages is described below as well as displayed in tabular and graphical formats (Figure 3.2).

3.5.2.1. All Life Stages

Unlike many other fish, Arctic grayling can tolerate low DO levels (Eriksen 1975 cited in Hubert et al. 1985). In laboratory conditions, the critical minimum DO for YOY and adults ranged between 1.4 – 2.0 $mg \cdot L^{-1}$ and 1.7 – 2.2 $mg \cdot L^{-1}$, respectively, at water temperatures ranging between 6 – 20 °C (Feldmuth and Eriksen 1978 cited in Hubert et al. 1985; McLeay et al. 1983 cited in Stewart et al. 2007a). Given the data, any DO level below the lowest critical DO of 1.4 $mg \cdot L^{-1}$ is not inhabitable (Index = 0). As adults appeared more sensitive than YOY, DO levels greater than the median critical DO for adults (2.0 $mg \cdot L^{-1}$) is optimal (Index = 1).

Dissolved Oxygen ($mg \cdot L^{-1}$)	Suitability Index
0	0
1.4	0
2.0	1.0
>2.0	1.0

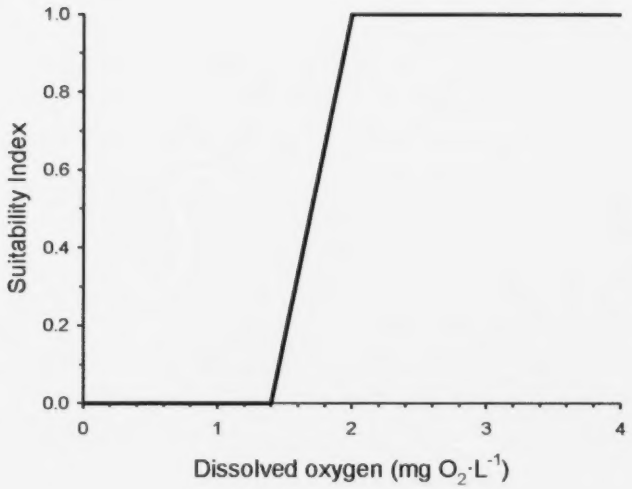

Figure 3.2. Habitat suitability curve of all life stages of Arctic grayling (*Thymallus arcticus*) at different dissolved oxygen levels ($mg \cdot L^{-1}$).

3.5.3. Water Temperature

Fish, being ectotherms, are greatly influenced by water temperature. For instance, water temperature can alter the rate of metabolic related activities as well as potentially trigger certain activities (e.g., migration, spawning). The majority of data obtained were temperature ranges in which spawning occurs and adults inhabit. Water temperature ranges were sparse for YOY and juveniles. CTMs were not incorporated into the model as fish behaviourally avoid water temperatures above thermal maximums. Given that water temperature affects ectotherms in any period of their life and at all times of the year, an HSI curve was developed that is suitable for all life stages and BSPs of Arctic grayling. The HSI curve for all life stages is described below[1] as well as displayed in tabular and graphical formats (Figure 3.3).

3.5.3.1. All Life Stages

Arctic grayling, conditioned to living in northern parts of North America, can withstand temperatures as low as 0.3 °C (Index = 0; Stewart et al. 2007a). Using medians, optimal water temperatures (Index = 1.0) for Arctic grayling was determined to be between 5 – 12 °C (compilation from Scott and Crossman 1973, Hubert et al. 1985, Ford et al. 1995, Northcote 1995, Evans et al. 2002, and Stewart et al. 2007a,). Adult Arctic grayling become stressed

around 17 °C and habitat is sub-optimal (Index = 0.5; Nelson and Wojcik 1953, Wojcik 1955 cited in Hubert et al. 1985). Adults actively avoid temperatures greater than 20 °C and habitat is not optimal (Index = 0; Wojcik 1955 cited in Hubert et al. 1985).

[1]The amount of information was uneven between life stages (especially lacking for YOY and juveniles while spawning had an excessive amount) and the maximum range was driven by the available data for adults. As such, optimal temperatures and the maximum range may be higher than reported here, as it would be skewed from the spawning and adult temperature data. Also, from the CTMs, it appears juveniles can withstand greater temperatures than adults; however, there was not enough optimal temperature data to support this notion.

Water Temperature (°C)	Suitability Index
0.3	0
5	1
12	1
17	0.5
20	0
> 20	0

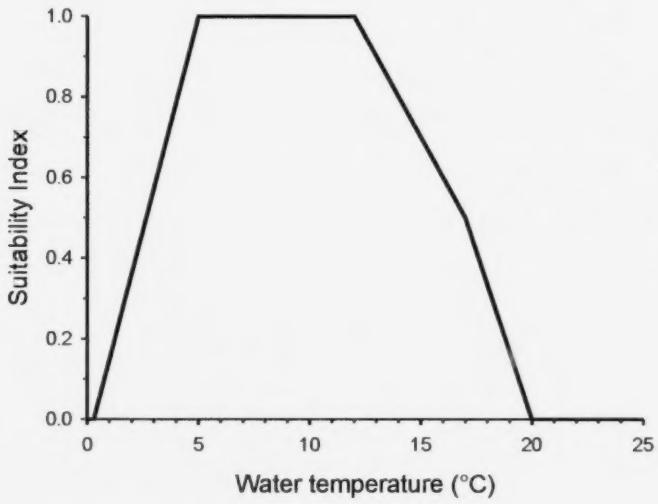

Figure 3.3. Habitat suitability curve of all life stages of Arctic grayling (*Thymallus arcticus*) at different water temperatures (°C).

3.5.4. Water Velocity

Water velocity is an important habitat component for stream-dwelling fish. As such, there was sufficient data available from the literature to create HSI curves for all four life stages. Most of the data compiled for water velocity preferences were given in ranges. Water velocity is considered to be mean column velocity. Any measures given in surface velocity was converted to mean column velocity using a factor of 0.85.

3.5.4.1. Spawning

The water velocity HSI curve for spawning will be applicable from the time adults arrive at spawning sites (roughly April) until the eggs hatch and YOY emerge (ca. mid July). The HSI curve for spawning is described below as well as displayed in tabular and graphical formats (Figure 3.4).

Spawning Arctic grayling have been found in water velocities as low as 0.3 $m \cdot s^{-1}$ (Index = 0; Stewart et al. 2007a). Using medians from a compilation of Hubert et al. (1985), Northcote (1995), Blackman (2002), Evans et al. (2002), and Stewart et al. (2007a), optimal water velocities (Index = 1.0) occur between 0.34 – 1.19 $m \cdot s^{-1}$. Spawning Arctic grayling were not found in velocities greater than the 1.46 $m \cdot s^{-1}$ and is not considered suitable habitat (Index = 0; Kreuger 1981 cited in Hubert et al. 1985).

Water Velocity ($m \cdot s^{-1}$)	Suitability Index
0.3	0
0.34	1.0
1.19	1.0
1.46	0
> 1.46	0

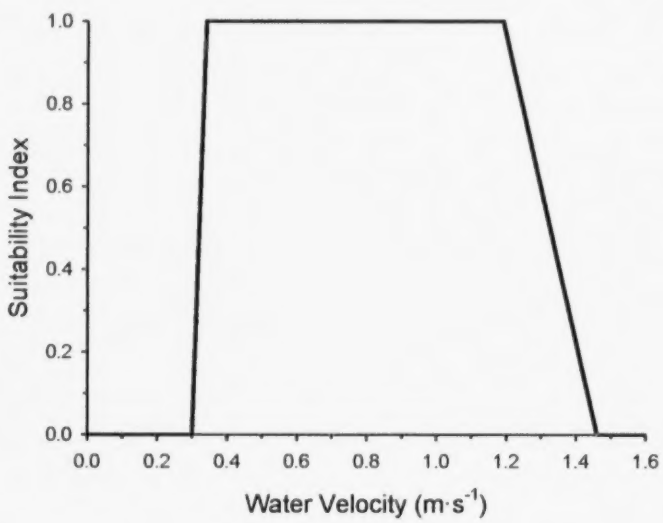

Figure 3.4. Habitat suitability curve of spawning Arctic grayling (*Thymallus arcticus*) at different water velocities ($m \cdot s^{-1}$).

3.5.4.2. YOY

The water velocity HSI curve for YOY will be applicable from the time YOY emerge until they migrate to overwinter. The HSI curve for YOYs is described below[2] as well as displayed in tabular and graphical formats (Figure 3.5).

The lowest velocity that YOY Arctic grayling were found in was 0 $m \cdot s^{-1}$ (compilation from Hubert et al. 1985 and Stewart et al. 2007a), coinciding with the median low range water velocity preference. Using medians, optimal water velocities (Index = 1.0) for YOYs are between 0 – 0.15 $m \cdot s^{-1}$ (compilation from Hubert et al. 1985, Blackman and Hunter 2001, Blackman 2002, Evans et al. 2002, Jones et al. 2003b, Blackman 2004, Deegan et al. 2005, and Stewart et al. 2007a). YOY Arctic grayling were not found in velocities greater than 0.8 $m \cdot s^{-1}$, which is not considered unsuitable habitat (Index = 0; Evans et al. 200, cited in Stewart et al. 2007a).

[2]The maximum velocity of 0.8 $m \cdot s^{-1}$ could not be confirmed from original sources and seems suspiciously high, which may be a misinterpretation of velocities that juveniles may encounter.

Water Velocity ($m \cdot s^{-1}$)	Suitability Index
0	1.0
0.15	1.0
0.8	0
> 0.8	0

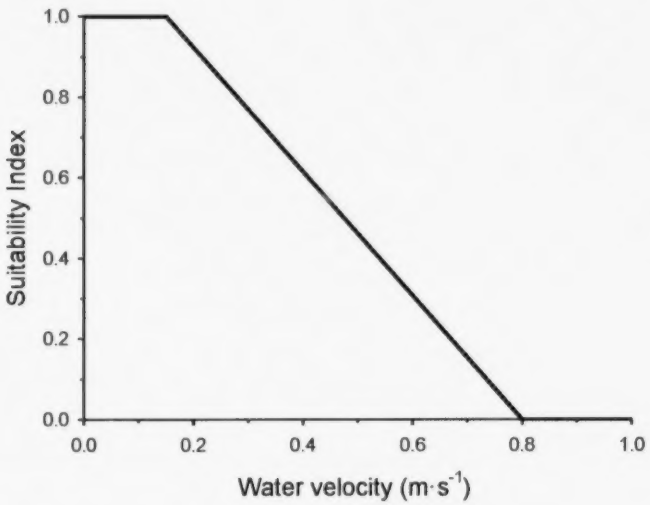

Figure 3.5. Habitat suitability curve of young-of-year Arctic grayling (*Thymallus arcticus*) at different water velocities ($m \cdot s^{-1}$).

3.5.4.3. Juveniles

The HSI curve for juveniles described below[3] is applicable during the summer months (Figure 3.6). The lowest velocity that juvenile Arctic grayling were found in was 0 $m \cdot s^{-1}$ (Evans et al. 2002), coinciding with the median low range water velocity preference. Using medians, optimal

water velocities (Index = 1.0) for juveniles is between 0 – 0.25 $m \cdot s^{-1}$ (compilation from Hubert et al. 1985, Ford et al. 1995, Blackman and Hunter 2001, Evans et al. 2002, and Stewart et al. 2007a). Juvenile Arctic grayling were not found in velocities greater 0.5 $m \cdot s^{-1}$, which was considered unsuitable habitat (Index = 0; Ford et al. 1995).

[3]Note that data was sparse so the water velocity HSI curve for juveniles may not fully illustrate their range of inhabitable velocities.

Water Velocity ($m \cdot s^{-1}$)	Suitability Index
0	1.0
0.25	1.0
0.5	0
> 0.5	0

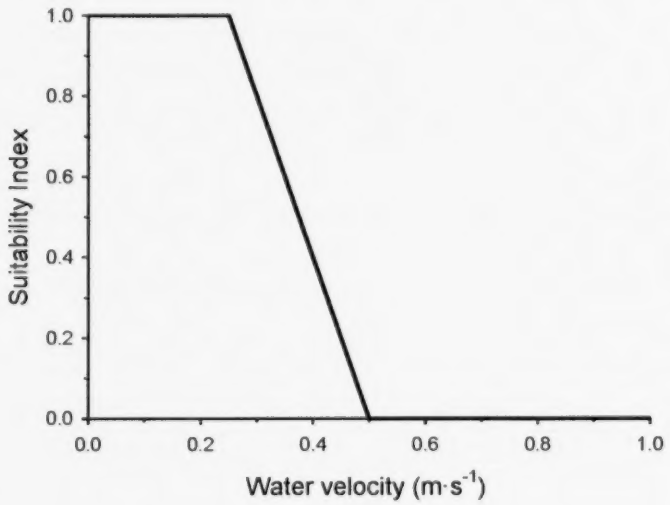

Figure 3.6. Habitat suitability curve of juvenile Arctic grayling (*Thymallus arcticus*) at different water velocities ($m \cdot s^{-1}$).

3.5.4.4. Adults

The summer HSI curve for adults is described below (Figure 3.7). Adult Arctic grayling have been found in water velocities as low as 0 $m \cdot s^{-1}$ and is the threshold for inhabitable waters (Index = 0; Evans et al. 2002; Blackman 2004). Using medians from a compilation of Hubert et al. (1985), Ford et al. (1995), Evans et al. (2002), Blackman 2004, and Stewart et al. (2007a), optimal water velocities occur between 0.25 – 0.9 $m \cdot s^{-1}$. Adult Arctic grayling were not found in velocities greater than 1.5 $m \cdot s^{-1}$ which is not considered suitable habitat (Index = 0; Stewart et al. 2007a).

Water Velocity ($m \cdot s^{-1}$)	Suitability Index
0	0
0.25	1.0
0.9	1.0
1.5	0
> 1.5	0

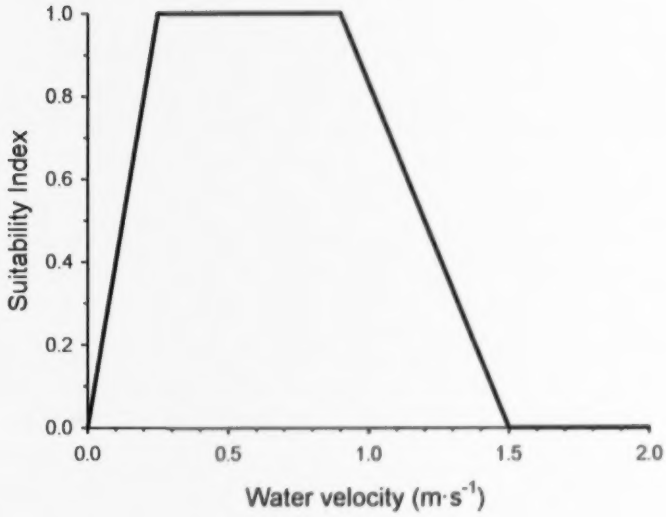

Figure 3.7. Habitat suitability curve of adult Arctic grayling (*Thymallus arcticus*) at different water velocities ($m \cdot s^{-1}$).

3.5.5. Depth

Water depth is a common habitat component recorded for fish, which allowed for sufficient data to be collected from the literature and create HSI curves for all four life stages of Arctic grayling. Most of the data compiled for water depth preferences were given in ranges.

3.5.5.1. Spawning

The water depth HSI curve for spawning will be applicable from the time adults arrive at spawning sites (roughly April) until the eggs hatch and YOY emerge (ca. mid July). The HSI curve for spawning is described below[4] as well as displayed in tabular and graphical formats (Figure 3.8).

Spawning adults and eggs were recorded to occur in waters as shallow as 0.10 m (Index = 0; Stewart et al. 1982 cited in Northcote 1995). Median ranges indicated that optimal water depths (Index = 1.0) for Arctic grayling are between 0.15 – 0.91 m (compilation from Bishop 1971, Hubert et al. 1985, Northcote 1995, Richardson et al. 2001, Blackman 2002, and Stewart et al. 2007a). Spawning adults and eggs were not found to occur in water deeper than 1 m (Index = 0; Tack 1972 and Bishop 1967 cited by Stewart et al. 2007a).

[4]Depth may not be important for spawning (Richardson et al. 2001).

Water Depth (m)	Suitability Index
0.10	0
0.15	1.0
0.91	1.0
1.00	0
> 1.00	0

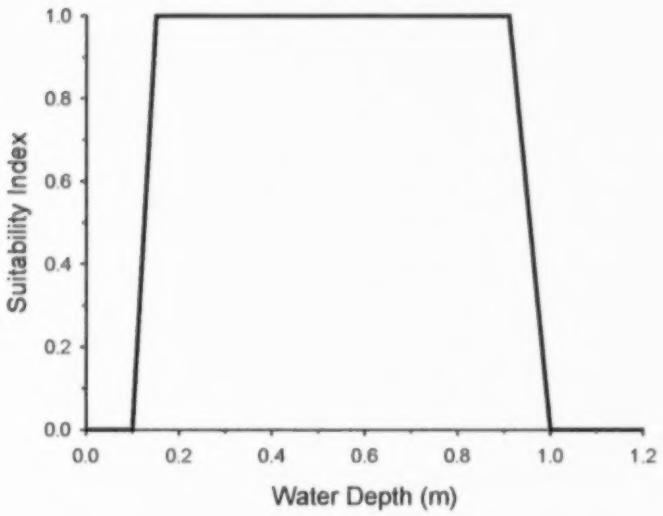

Figure 3.8. Habitat suitability curve of spawning Arctic grayling (*Thymallus arcticus*) at different water depths (m).

3.5.5.2. YOY

The water depth HSI curve for YOY will be applicable from the time YOY emerge until they migrate to overwinter. The HSI curve for YOYs is described below as well as displayed in tabular and graphical formats (Figure 3.9).

The shallowest depth that YOY Arctic grayling were found in was 0 m (Roberge et al. 2002). Median ranges indicated that optimal water depths (Index = 1.0) for YOYs are between 0.08–0.45 m (compilation from Hubert et al. 1985, Blackman and Hunter 2001, Blackman 2002, Evans et al. 2002, Jones et al. 2003b, Roberge et al. 2002, Deegan et al. 2005, and Stewart et al. 2007a). YOY Arctic grayling were not found in water deeper than 0.85 m which was not considered suitable habitat (Index = 0; Elliott 1980 cited in Hubert et al. 1985).

Water Depth (m)	Suitability Index
0	0
0.08	1.0
0.45	1.0
0.85	0
> 0.85	0

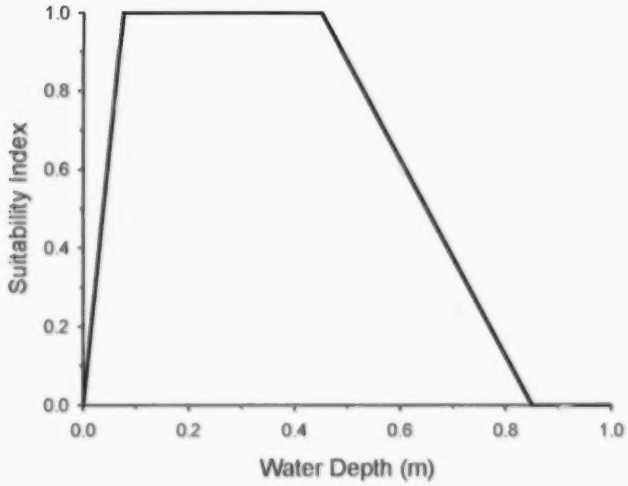

Figure 3.9. Habitat suitability curve of young-of-year Arctic grayling (*Thymallus arcticus*) at different water depths (m).

3.5.5.3. Juveniles

The water depth HSI curve for juveniles is applicable during the summer months when not overwintering or migrating. The HSI curve for juveniles is described below as well as displayed in tabular and graphical formats (Figure 3.10).

The shallowest depth that juvenile Arctic grayling were found in was 0.2 m (Richardson et al. 2001, Evans et al. 2002, Stewart et al. 2007a), coinciding with the median low range water depth preference. Median ranges indicated that optimal water depths (Index = 1.0) for juveniles is between 0.2 – 0.8 m (compilation from Hubert et al. 1985, Ford et al. 1995, Blackman and Hunter 2001, Richardson et al. 2001, Blackman 2002, Evans et al. 2002, and Stewart et al. 2007a,). Juvenile Arctic grayling were not found in water deeper than 1.16 m, which was not considered suitable habitat (Index = 0; Kreuger 1981 cited in Hubert et al. 1985).

Water Depth (m)	Suitability Index
0.2	0
0.2	1.0
0.8	1.0
1.16	0
> 1.16	0

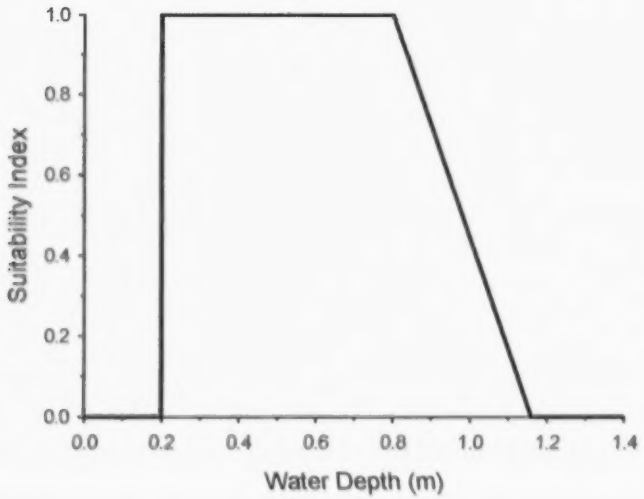

Figure 3.10. Habitat suitability curve of juvenile Arctic grayling (*Thymallus arcticus*) at different water depths (m).

3.5.5.4. Adults

Similar to juveniles, the water depth HSI for adults is applicable during the summer months when adults are not overwintering, migrating or spawning. The HSI curve for adults is described below as well as displayed in tabular and graphical formats (Figure 3.11).

Adult Arctic grayling have been found in depths as low as 0.2 m and is considered the threshold for inhabitable waters (Index = 0; Kreuger 1981 cited in Hubert et al. 1985). Median ranges from a compilation of Hubert et al. (1985), Ford et al. (1995), Evans et al. (2002), Roberge et al. (2002), Blackman (2004), and Stewart et al. (2007a) indicate that optimal water depths occur between 0.5 – 1.34 m. Adult Arctic grayling were not recorded to occur in water depths greater than 2.8 m which is not considered suitable habitat (Index = 0; Blackman 2004).

Water Depth (m)	Suitability Index
0	0
0.2	0
0.5	1.0
1.34	1.0
2.8	0
> 2.8	0

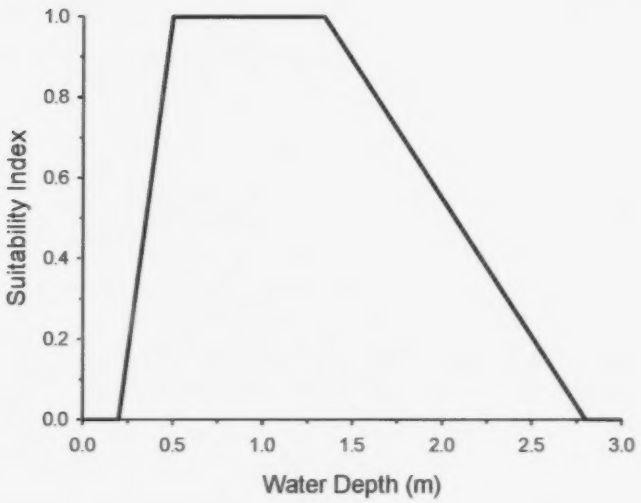

Figure 3.11. Habitat suitability curve of adult Arctic grayling (*Thymallus arcticus*) at different water depths (m).

3.5.6. Substrate

Substrate type is another common habitat component recorded for fish which allowed for sufficient data to be collected from the literature and determine HSIs for all four life stages of Arctic grayling. Most of the data listed the various substrates that each life stage occurred in. Frequency of each substrate category was enumerated and preference was determined. Substrate type was recorded as stated by cited authors, else substrate was classified by particle size similar to Stewart et al. (2007a): bedrock = uniform continuous substrate; boulder = >25 cm; cobble = 17–<25 cm; rubble = 6.4–<17 cm; gravel = 0.2–<6.4 cm; sand = <0.2 cm; silt/clay = finer than sand with fine organic content; muck (detritus) = mud with coarse organic content; hard-pan clay = clay; and pelagic = open water.

Substrate type HSIs are applicable to lotic environments during the BSP that each respective life stage occurs in, except for periods of migrating and overwintering, and in the case with adults, spawning. The HSI curve for all life stages is described below as well as in tabular and graphical format (Table 3.1; Figure 3.12). In general, Arctic grayling are strongly associated with gravel for all life stages.

3.5.6.1. Spawning

Gravel is particularly important as a spawning substrate. However, Arctic grayling will spawn over other substrates such as boulder, cobble, rubble, sand, silt, and mud, although it is sub-optimal to gravel (compilation of Tack 1972, 1980, Hubert et al. 1985, Ford et al. 1995, Northcote 1995, Evans et al. 2002, and Stewart et al. 2007a).

3.5.6.2. YOY

YOY preference is typically gravel and fine sediments (silt, sand) associated with slower habitat types yet they also associate strongly with cobble, and to a lesser extent boulder and rubble (compilation of Ford et al. 1995, Northcote 1995, Blackman 2002, Evans et al. 2002, Cowie and Blackman 2007, and Stewart et al. 2007a).

3.5.6.3. Juvenile

Juveniles had a strong preference for gravel with cobble. Juveniles will sometimes occur amongst boulders, sand, and silt, and less occasionally with rubble (compilation of Ford et al. 1995, Blackman 2002, and Stewart et al. 2007a).

3.5.6.4. Adult

Adults were primarily associated with gravel, and some rubble, cobble, and boulders (compilation of Ford et al. 1995 and Stewart et al. 2007a).

Table 3.1. Habitat suitability for each life stage of Arctic grayling (*Thymallus arcticus*) with different substrate types.

	Life Stage			
Substrate	Spawn	YOY	Juvenile	Adult
Granite	0	0	0	0
Boulder	0.33	0.6	0.5	0.5
Cobble	0.17	1.0	0.75	0.5
Rubble	0.25	0.6	0.25	0.5
Gravel	1.0	1.0	1.0	1.0
Sand	0.17	0.8	0.5	0
Silt	0.08	1.0	0.5	0
Mud	0.08	0	0	0

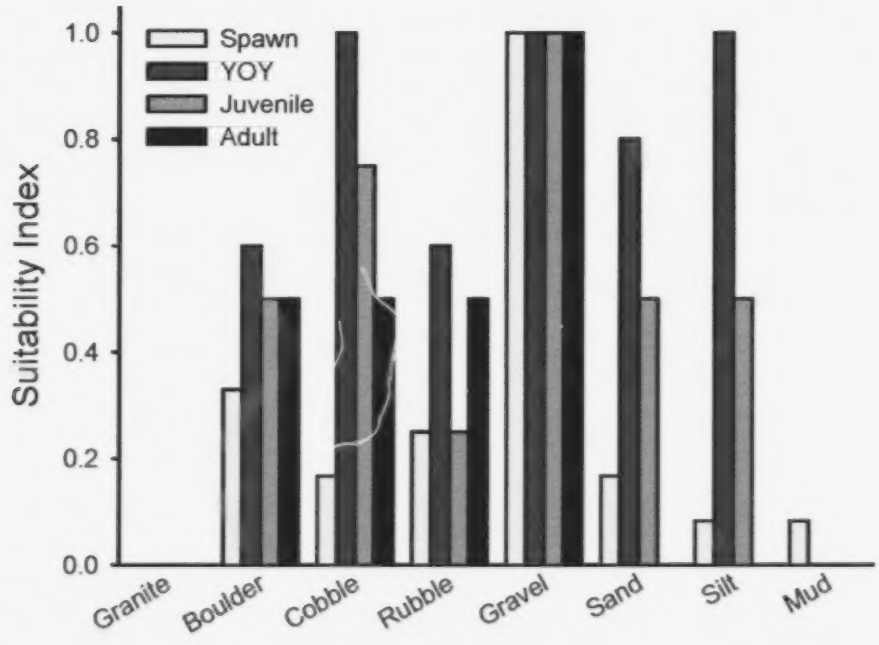

Figure 3.12. Habitat suitability for each life stage of Arctic grayling (*Thymallus arcticus*) with different substrate types.

3.5.7. Cover

Cover is not as commonly recorded for fish as substrate as a habitat component. Although data was not always sufficient, it was too variable between life stages to compile together. As such, HSIs were determined for all four life stages of Arctic grayling. Most of the data compiled listed the various cover that each life stage utilizes. Frequency of each cover category was enumerated and preference was determined for cover used.

Cover HSIs are applicable to lotic environments during the BSP that each respective life stage occurs in, except for periods of migrating and overwintering, and in the case of adults, spawning. The HSIs are described below for each life stage and is displayed in tabular and graphical format (Table 3.2; Figure 3.13).

3.5.7.1. Spawning

There has been no mention of cover used when spawning, so it is assumed that no cover is required (Hubert et al. 1985).

3.5.7.2. YOY

Young-of-year Arctic grayling can easily find cover in the substrate (the interstitial space between any substrate size (boulder – sand)) due to their small size and this is the most preferred cover for this age group. Overhead cover (such as overhanging vegetation) is also known to be used by YOY on occasion (compilation of Hubert et al. 1985, Evans et al. 2002, and Stewart et al. 2007a).

3.5.7.3. Juvenile

Juveniles will often use rocks or other substrate as cover. However, they will occasionally use overhead or *in situ* cover (submerged cavities and/or crevices, and undercut banks), and there is mention of using logs as cover (compilation of Hubert et al. 1985 and Stewart et al. 2007a).

3.5.7.4. Adult

Variable cover types have been recorded for adult Arctic grayling. However, using substrate was the most preferred. Aside from substrate, adults will often use deep pools to hide as well as overhead cover. Rarely will they use emergent and submergent vegetation, *in situ* or no cover at all (compilation of Suchanek et al. 1984, Evans et al. 2002, Blackman 2004, and Stewart et al. 2007a).

Table 3.2. Habitat suitability for each life stage of Arctic grayling (*Thymallus arcticus*) with different types of cover.

	Life Stage			
Cover	Spawn	YOY	Juvenile	Adult
Substrate	0	1.0	1.0	1.0
Overhead	0	0.25	0.25	0.67
Deep pool	0	0	0	0.67
None	1.0	0	0	0.33
In situ	0	0	0.25	0.33
Emergent vegetation	0	0	0	0.33
Submergent vegetation	0	0	0	0.33
Wood	0	0	0.25	0

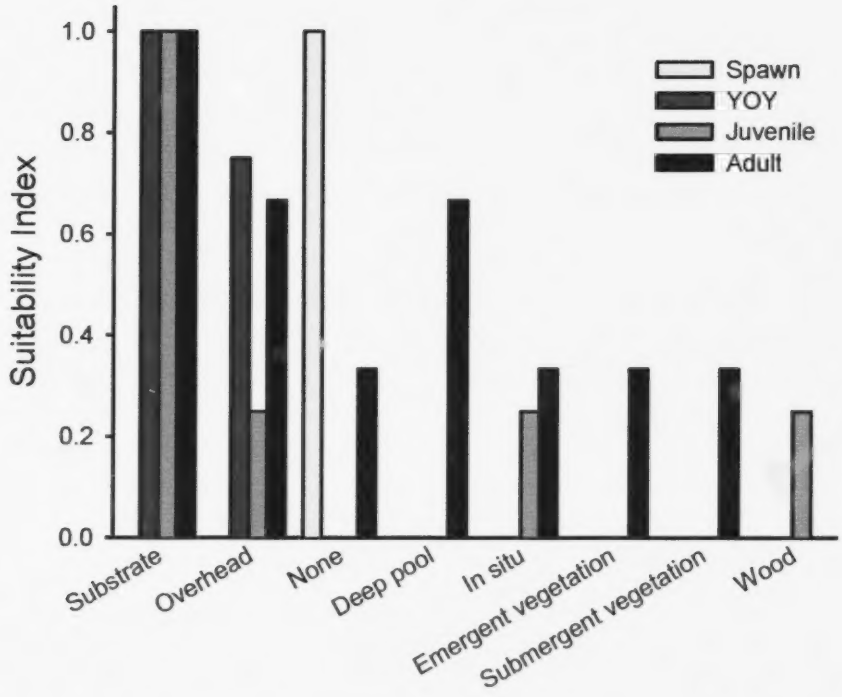

Figure 3.13. Habitat suitability for each life stage of Arctic grayling (*Thymallus arcticus*) with different types of cover.

3.5.8. Habitat Type

Habitat type is a relatively common habitat component recorded for fish, which allowed for sufficient data to be collected from the literature to determine HSIs for all four life stages of Arctic grayling. Most of the data compiled listed the various habitats that each life stage occurred in. The frequency of each habitat category was enumerated and preference was determined. In flowing water, habitat refers to the type of channel unit (sometimes typified by water velocity and turbulence). For simplicity and consistency between references, runs and glides were combined. When the literature indicated "below riffles" it was interpreted as a run/glide.

Habitat type HSIs are applicable to lotic environments during the BSP that each respective life stage occurs in, except for periods of migrating and overwintering, and in the case of adults, spawning. The HSIs are described below for each life stage and is displayed in tabular and

graphical format (Table 3.3; Figure 3.14). Habitat type preferences appear to correspond well with previously described velocities and substrate preferences for each life stage.

3.5.8.1. Spawning

Spawning occurs primarily in riffles and frequently in runs where water velocity is relatively fast (Bishop 1967; Tack 1980; Hubert et al. 1985; Ford et al. 1995; Northcote 1995; Evans et al. 2002; Stewart et al. 2007a). Spawning grayling will often hold in pools (Evans et al. 2002). Otherwise, spawning has occurred in various habitats, including off-channels (habitat that is outside the mainstem flow including side channels, backwaters, and off channel habitats, which is often of low velocity or still water), and highway culverts (Northcote 1995; Evans et al. 2002).

3.5.8.2. YOY

YOY are mostly associated with slow habitats such as off-channels (side-channels and backwaters) and river margins (Tack 1980; Ford et al. 1995; Northcote 1995; Stewart et al. 2007a). YOY Arctic grayling will also be found, albeit to a lesser extent, in quiet pools and shallow riffles (Ford et al. 1995; Stewart et al. 2007a).

3.5.8.3. Juvenile

Juveniles are primarily associated with pools but are also associated with slower moving habitat such as off-channels and river margins and to a lesser extent runs and riffles (Hubert et al. 1985; Ford et al. 1995; Northcote 1995; Blackman 2002; Evans et al. 2002; Stewart et al. 2007a).

3.5.8.4. Adult

Lastly, adults are also mostly associated with pools in which they preferably feed but are also found occasionally in runs (Hubert et al. 1985; Hughes and Dill 1990; Ford et al. 1995; Northcote 1995; Blackman 2002, 2004).

Table 3.3. Habitat suitability for each life stage of Arctic grayling (*Thymallus arcticus*) with different types of river habitat.

	Life Stage			
Habitat Type	Spawn	YOY	Juvenile	Adult
Riffles	1	0.14	0.14	0
Runs	0.8	0	0.29	0.6
Pools	0.4	0.29	1	1
River margin	0	0.71	0.43	0
Off-channel	0.2	1	0.43	0
Other	0.2	0	0	0

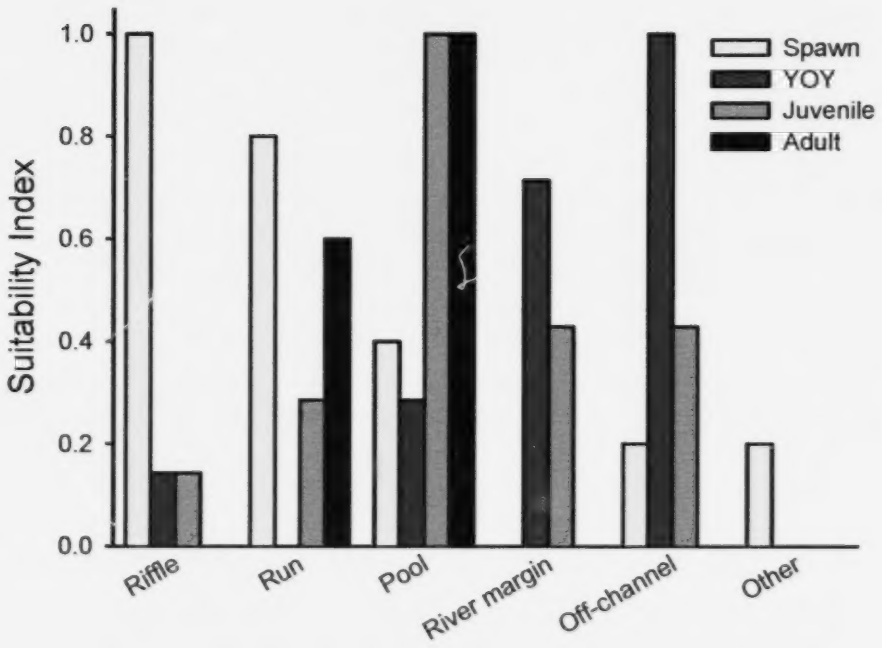

Figure 3.14. Habitat suitability for each life stage of Arctic grayling (*Thymallus arcticus*) with different types of river habitat.

3.6. DATA GAPS

Some areas in which there was a paucity of information includes *temperature* preferences, *juvenile water velocity* preferences, *turbidity* value preferences, minimum *dissolved oxygen* capabilities, use of *cover*, and especially any of the variables pertaining to the *overwintering* BSP.

3.7. COMPOSITE HSI

The different methods to create a composite HSI from the individual variable suitability indices will each produce different estimates of habitat suitability (Jowett and Davey 2007). The most basic methods to compose composite HSIs are from using either the product, arithmetic mean, or geometric mean of the individual HSIs (Vadas and Orth 2001; Ahmadi-Nedushan et al. 2006). More complex methods exist to determine the composite HSI (see Ahmadi-Nedushan et al. 2006). However, all composite indices must contend with assumptions regarding how the individual suitability indices are combined. The basic composite HSIs are often utilized in part from their simplicity but also because they can easily be incorporated into modeling programs such as ArcGIS, PHABSIM, and River2D (e.g., Brown et al. 2000; Beecher et al., 2002; Haxton et al. 2008; Tirpak et al. 2009; Lee et al. 2010). The geometric mean (n^{th} root of the product of n individual indices) allows for one variable to compensate for the poor conditions of other variables, yet can yield zero if any variable has a zero HSI (Brown et al. 2000). However, using a technique by Oldham et al. (2000), if individual HSI scores are set to a minimum of 0.01 instead of zero it can reflect the possibility that under unusual circumstances, Arctic grayling could occur in such an area. This may be more optimal for conditions which may not absolutely drive a habitat to have zero suitability (e.g., velocity, depth, substrate, cover, habitat type).

The composite HSI for Arctic grayling was calculated using the geometric mean. Velocity, depth, substrate, cover, and habitat type will have a minimum HSI score of 0.01. Variables that are thought to limit Arctic grayling occurrence such as turbidity, temperature, and DO will have a minimum HSI score of 0. Using the geometric mean to calculate the composite HSI assumes the following:

- All variables are equally important in contributing to the overall habitat suitability and fitness of Arctic grayling (de Kerckhove et al. 2008; Beecher et al. 2002). For instance, turbidity is as important as cover type.
- Habitat variables do not interact and correlate in any way (de Kerckhove et al. 2008; Beecher et al. 2002). This is a common assumption, which HSIs are often criticized for (Ahmadi-Nedushan et al. 2006). For example, stream velocity often influences the size and composition of the substrate, and velocity and depth also tend to be highly correlated (Jowett 2003; Ahmadi-Nedushan et al. 2006).

The composite HSI is presented below which is to be calculated for the specific life stage (ls) of interest. Variable types are superscripted for each HSI and the specific life stage (ls) is subscripted.

$$Composite\ HSI_{ls} = \left(HSI_{ls}^{turbidity} + HSI_{ls}^{oxygen} + HSI_{ls}^{water\ temperature} + HSI_{ls}^{water\ velocity} + HSI_{ls}^{depth} + HSI_{ls}^{substratre} + HSI_{ls}^{cover} + HSI_{ls}^{habitat\ type}\right)^{1/8}$$

4. BIOENERGETICS

4.1. OVERVIEW

Bioenergetics models are different from HSIs in that they use the physiology of the species to objectively quantify and evaluate habitat quality. Unlike HSIs, bioenergetics models are easily related to true habitat quality as the model directly estimates fitness consequences in the form of fish tissue growth or net energy gain (Rosenfeld 2003; de Kerckhove et al. 2008). Other than directly estimating fitness consequences, bioenergetics incorporates food availability into the model. Food availability is a variable that drives many of the physical variable preferences for a species seen in HSIs. However, if two streams were similar in velocity, depth, and substrate composition, yet one stream has a significantly greater supply of macroinvertebrates for drift-feeding fish, then the stream with more macroinvertebrates will support more fish (Jones et al. 2003a). The HSI based on physical variables would not differentiate between streams, while the bioenergetics model would differentiate the streams based on food availability and estimated net energy intake or growth. Thus, there has been evidence that bioenergetics models can potentially be better predictors of habitat suitability than HSI curves (Rosenfeld et al. 2005).

The overall idea behind linking bioenergetics models to habitat quality relies on a few basic concepts. Foremost, bioenergetics models are based on the simple equation (de Kerckhove et al. 2008):

(Eq. 1) $$Net\ Energy = Energy\ Ingested - (Energy\ Expenditure\ and\ Losses)$$

The Net Energy in the equation typically goes towards somatic and/or gonadal growth, and can easily be converted into a growth rate (de Kerckhove et al. 2008). Growth rate, as a fitness

consequence, is then the estimation of habitat quality and ecosystem productivity. The other parts of the equation are relatively straightforward. Energy Ingested is the energy consumed by the organism, typically in the form of prey. The other half of the equation involves energy loss through metabolic and physiological processes. Energy Expenditure refers to metabolic demands and energetic costs associated with activity (i.e., swimming costs), digestion (i.e., specific dynamic action; SDA), and respiration (i.e., standard metabolic rate). Finally, the Losses part of the equation refers to the consumed energy that cannot be assimilated and is released through excretion and egestion. In its most basic form, bioenergetics models take food availability and subtract costs from metabolic and physiological processes to estimate growth, which in turn quantifies habitat quality.

Bioenergetics modelling requires a lot of data on known metabolic and physiological relationships. As such, rare species are difficult to model as little information exists for them. Instead, bioenergetics models are typically restricted to well-studied species, particularly of economic importance (e.g., drift-feeding salmonids). Also, due to high information needs, bioenergetics models have mostly been utilized at the microhabitat scale to determine habitat selection (e.g., Fausch 1984; Hughes and Dill 1990; Hughes 1992), while few bioenergetics models have been applied at larger scales (e.g., Hughes 1998; Rosenfeld and Boss 2001). However, as information is collected over time, more recent bioenergetics models have been utilized to determine habitat suitability (Nislow et al. 2000; Guensch et al. 2001; Rosenfeld et al. 2005; Jenkins and Keeley 2010). Given the increased availability of information, we were able to develop a bioenergetics model to determine habitat suitability for the well-studied Arctic grayling within and among streams, as discussed below.

4.2. LIFE STAGE SPECIFIC MODELS

The bioenergetics model was conducted for three life stages of Arctic grayling: YOY, juveniles, and adults. Each life stage varies in size and metabolic requirements and will exhibit different outcomes for optimal habitat. Therefore, it is important to distinguish each life stage separately.

The bioenergetics model distinguishes life stages by differences in length and weight. We use fork length, which is a more commonly reported measure than weight, to separate each life stage.

YOYs can range from 1 cm (at emergence) to 15 cm (by end of the year) but more typically between 1 – 8 cm (Hubert et al. 1985; Northcote 1993; Jones et al. 2003a). Thus, we used the mid-point of 5 cm for the YOY model. Juveniles have been reported between the sizes 7 – 30 cm (Northcote 1993; Bishop 1967) and an approximate mid-point of 15 cm was used for the juvenile model. Adults typically range between 30-38 cm and can get up to 70 cm (Scott and Crossman 1973). We used 35 cm fork length for the adult model.

The Arctic grayling bioenergetics model is applicable to lotic environments during the BSP when each of the three life stages is feeding (e.g. summer months). Thus, the model does not apply to periods of migrating and overwintering, and in the case of adults, spawning.

Assumption: Metabolic costs for YOY, juveniles, and adults are similar, aside from differences caused by size (e.g., disregard that YOY tend to have greater metabolism when controlling for size).

4.3. BASIC BIOENERGETICS MODEL

As previously indicated, bioenergetics models start with a basic equation (Eq. 1) to obtain net energy. For the Arctic grayling model a modified version of the basic equation will be used:

(Eq. 2) $$NEI = GEI - SC$$

where NEI is Net Energy Intake ($J \cdot h^{-1}$), GEI is Gross Energy Intake ($J \cdot h^{-1}$), and SC is Swimming Costs ($J \cdot h^{-1}$; Hughes and Dill 1990; Rosenfeld and Boss 2001). The same basic model components are involved, except GEI combines the energy gained from consumption and metabolic and maintenance costs other than costs from metabolic activity (i.e., swimming).

4.4. ENERGETIC COSTS

The metabolic costs of fish is a combination of their standard metabolic rate (the energy equivalent of a resting, unfed fish), the energy required for swimming or other activities, and the energy required for digestion and maintenance (SDA; Elliott 1976). Arctic grayling are drift-feeding salmonids and constantly swim to maintain a position in the river to obtain food and are not "at rest" *per se* (O'Brien and Showalter 1993). Thus, swimming cost (SC) incorporates both

standard metabolic rate and activity rate (Rosenfeld and Boss 2001). The following equation developed by Hughes and Dill (1990) was used for swimming costs:

(Eq. 3) $$SC = 10^{(C+M\cdot V)} \cdot 19 \cdot \frac{FW}{1000}$$

where C = 2.07 – 0.37 · log(FL) and M = 0.410 – 0.0196 · log(FL) are dimensionless scalers, V is velocity ($cm \cdot s^{-1}$), FW is fish weight (g), and FL is fish length (cm). Hughes and Dill (1990) derived swimming costs for Arctic grayling from graphical models in Brett and Glass (1973) on sockeye salmon adjusted to 10 °C. Metabolism varies with temperature, however, tundra and mountain streams in which Arctic grayling are found are typically 8-12 °C during summer (Jones et al. 2003a; Deegan et al. 2005; Luecke and MacKinnon 2008). Thus, a model adjusted for 10 °C is appropriate for our purposes.

Assumption:

- The energetic cost of attacking prey is minimal and can be ignored, as in Hughes and Dill (1990).

Gross Energy Intake has some energetic costs associated with it as well:

(Eq. 4) $$GEI = E \cdot UE$$

where E is Energy Intake ($J \cdot h^{-1}$) and UE is Utilization Efficiency (a proportion of energetic intake).

Utilization Efficiency is a combination of the energetic costs required for digestion (SDA), as well as unassimilated energy released through faeces (F) and excretion (U).

(Eq. 5) $$UE = 1 - \left(\frac{SDA+F+U}{100}\right)$$

All the values, SDA, F, and U, are a percentage of the energetic intake. Specific Dynamic Action is typically 14% for fish in general (Brett and Groves 1979; Niimi and Beamish 1974 cited in Hill and Grossman 1993). Faeces and excretion are most often cited as 15% and 10%,

respectively, for generic fish (Jones et al. 2003a; Tucker and Rasmussen 1999). Thus, UE is assumed to be 0.61 for the Arctic grayling bioenergetics model.

Assumption:

- The components of UE are constant and do not vary with level of satiation, type of food, or life stage.

4.5. ENERGETIC GAINS

In the Arctic grayling bioenergetics model, all of the energetic gains come from consuming food. Energetic Intake is the energy from the consumption of prey within a given time frame, which is a factor of consumption rate and prey energy.

(Eq. 6) $$E = CR \cdot PE$$

where CR is consumption rate ($g \cdot h^{-1}$), and PE is prey energy ($J \cdot g^{-1}$). Although a generalist, Arctic grayling primarily consume aquatic invertebrates in the stream drift, with particular preference for chironomids, mayflies, and caddisflies. In terms of PE, the mean energetic value of the Arctic graylings top reported prey preferences was 22164 $J \cdot g^{-1}$ for each life stage (Cummins and Wuycheck 1971).

Assumption:

- The entire organism provides energy for the Arctic grayling (e.g., all parts such as chitin are digestible).
- The mean energetic value adequately estimates actual energetic values of prey for all life stages.

The CR of aquatic invertebrates in stream drift not only depends on prey abundance but also the search and handling time involved with capturing prey. Typically, Arctic grayling exhibit a type II functional response where as prey abundance increases, feeding increases at a steadily decreasing rate until it plateaus (O'Brien et al. 2001). The plateau in consumption is due to the time spent handling prey limiting the feeding capacity of the Arctic grayling at high prey

densities. As such, CR was calculated to follow a type II functional response using encounter rates (i.e., search time) and handling time (Hughes 1998).

(Eq. 7) $$CR = \frac{ER}{1+ER \cdot H} \cdot PM \cdot 60 \cdot 60$$

where ER is encounter rate (number of prey $\cdot s^{-1}$), H is handling time (s), PM is prey mass (g), and $60 \cdot 60$ is to convert seconds to hours.

The ER of prey can be estimated by the prey density that falls within the Arctic grayling's search area over a specified time. The search area is the area around a fish's stream position that they can capture prey combined with water velocity. Although fish maintain a position within the stream, they are constantly searching for prey in the unsearched water that flows past. Consequently, water velocity is positively correlated to ER.

(Eq. 8) $$ER = CA \cdot V \cdot PD \cdot 10^{-6}$$

where CA is capture area (cm^2), PD is prey density (number of prey $\cdot m^{-3}$), and 10^{-6} is to convert m^3 to cm^3 (Hughes and Dill 1990).

Finally, the handling time involved with consuming food, as calculated in Hughes (1998):

(Eq. 9) $$H = RD/Vmax$$

where RD is reactive distance (cm) and Vmax is Arctic grayling's maximum sustainable swimming speed ($cm \cdot s^{-1}$). An explanation for the derivation of the equation can be found in Hughes (1998). Handling time is quick in this model, as food is easily consumed and fish just need to return to their optimal position in the stream before catching more prey. This is an improvement from using only the encounter rate (e.g., Hughes and Dill 1990) as this model takes into account that prey densities may reach a level where capture success is not 100%.

Assumption:

- Capture success is 100% at lower prey densities.

4.6. OTHER VARIABLES

Some of the variables mentioned in the calculation of NEI were not fully introduced and are explained below.

The CA or drift foraging (search) window involves the area in which Arctic grayling are capable of searching and feeding within as they swim. This area via maximum capture distance (MCD) is reduced as velocity increases, albeit the encounter rate of prey increases with velocity (Hughes and Dill 1990; O'Brien and Showalter 1993). Depending on the depth of the stream, the CA can be an entire circle using MCD as the radius or variations of such an area (Hughes 1998). Jenkins and Keeley (2010) generalized the CA for cutthroat trout (*Oncorhynchus clarkii bouvieri*) to be a half circle using MCD as the radius or less than half a circle if stream depth (SD) was less than MCD. The equation for CA in Jenkins and Keeley (2010) takes into consideration any truncation of the area from the water surface. However, as Arctic grayling feed at mid-water depths (Stewart et al. 2007b), the model needed to allow for truncation of the CA from both the water surface and stream bottom. Thus, to consider these aspects, the CA equation for Arctic grayling was an adaptation from Hughes (1998) and Jenkins and Keeley (2010).

(Eq. 10)

$$If\ SD \geq 2 \cdot MCD, then$$

$$CA = \pi(MCD)^2$$

$$If\ SD < 2 \cdot MCD, then$$

$$CA = 2\left\{0.5 \cdot SD\left[\sqrt{MCD^2 - (0.5 \cdot SD)^2}\right] + MCD^2 \cdot \sin^{-1}\left(\frac{0.5 \cdot SD}{MCD}\right)\right\}$$

where SD is stream depth (cm) and MCD (cm) is the radius of the maximum capture area at a given velocity.

Assumption:

- The area between the stream bed and the fish's stream position is minimal.

The MCD is a combination of a fish's reactive distance to prey, the velocity in which prey is heading towards the fish, and the swimming speed which the fish can maintain. The derivation of the equation below for calculating MCD is further explained in Hughes and Dill (1990).

(Eq. 11) $$MCD = \sqrt{\left[(RD)^2 - \left(V \cdot \frac{RD}{Vmax}\right)^2\right]}$$

The RD is the distance in the water in which fish detect and react to prey. The RD varies with both the size of the prey and size of the fish. Both, larger prey and larger fish, increase the distance in which prey becomes detected.

(Eq. 12) $$RD = 12 \cdot PL\left[1 - e^{(-0.2 \cdot FL)}\right]$$

where PL is prey length (mm). The equation is derived from Hughes and Dill (1990).

Previous bioenergetics models have used multiple prey lengths (e.g., Hughes and Dill 1990; Rosenfeld and Boss 2001). However, to simplify, we used a single prey length of 4.5 mm, which is the estimated length of an Arctic grayling food item used in Hughes (1998). Knowing the length of the Arctic grayling's preferred prey would be more accurate, yet, these lengths could not be easily discerned from the literature.

Prey mass was calculated from prey length using a length/weight regression from Benke et al. (1999).

(Eq. 13) $$PM = 0.0064 \cdot PL^{2.788} \cdot 10^{-3}$$

where 10^{-3} is to convert mg to g.

The average weight of the Arctic grayling at each life stage's fork length was calculated using a length-weight regression equation adapted from graphical data presented in Bishop (1967). Other sources exist with Arctic grayling length-weight regressions (e.g., Hughes and Dill 1990; Dahlke 1983; Luecke and MacKinnon 2008; Craig and Poulin 1975; Ballard and Shrimpton 2009). However, data from Bishop (1967) fell within the mid-range of other regression equations and was obtained within the area that the model was developed for.

(Eq. 14) $$FW = 0.0224 \cdot FL^{2.8379}$$

Finally, Vmax, mentioned previously, was derived by Jones et al. (1974) for Arctic grayling.

(Eq. 15) $$Vmax = 36.23 \cdot FL^{0.19}$$

Jones et al. (1974) described Vmax as the critical velocity in which Arctic grayling can swim for at least 10 min. Typically, sustained swimming occurs for longer than 200 min, thus, the Vmax may be more representative of prolonged or burst swimming.

Assumption:

- Vmax is representative of sustainable swimming.

All of the above estimated variables and equations used in the Arctic grayling bioenergetics model are summarized in Table 4.1 and 4.2, respectively.

Table 4.1. Standard and estimated values for variables used in an Arctic grayling bioenergetics model to predict stream habitat quality.

Variable	Value
Specific Dynamic Action (%)	SDA = 14
Egestion (%)	F = 15
Excretion (%)	U = 10
Prey Energy ($J \cdot g^{-1}$)	PE = 22164
Prey length (mm)	PL = 4.5
Fish Fork Length (cm)	FL = 5 for young-of-years FL = 15 for juveniles FL = 35 for adults

Table 4.2. Equations used by the Arctic grayling bioenergetics model to estimate stream habitat quality.

Variable	Equation	Source
Net Energy Intake ($J \cdot h^{-1}$)	$Net\ Energy = Energy\ Ingested - (Energy\ Expenditure\ and\ Losses)$	
Swimming Cost ($J \cdot h^{-1}$)	$SC = 10^{(C+M \cdot V)} \cdot 19 \cdot \frac{FW}{1000}$ $Where\ C = 2.07 - 0.37 \cdot log(FL)\ and\ M = 0.0410 - 0.0196 \cdot log(FL)$	Hughes and Dill (1990)
Gross Energy Intake ($J \cdot h^{-1}$)	$GEI = E \cdot UE$	
Utilization Energy	$UE = 1 - (SDA + F + U)/100$	
Energy Intake ($J \cdot h^{-1}$)	$E = CR \cdot PE$	
Consumption Rate($g \cdot h^{-1}$)	$CR = \frac{ER}{1 + ER \cdot H} \cdot PM \cdot 60 \cdot 60$	Hughes (1998)
Encounter Rate (number of prey$\cdot s^{-1}$)	$ER = CA \cdot V \cdot PD \cdot 10^{-6}$	Hughes and Dill (1990)
Handling time (s)	$H = RD/Vmax$	Hughes (1998)
Capture area (cm^2)	$If\ SD \geq 2 \cdot MCD, then$ $CA = \pi(MCD)^2$ $If\ SD < 2 \cdot MCD, then$ $CA = 2\left\{0.5 \cdot SD\left[\sqrt{MCD^2 - (0.5 \cdot SD)^2}\right] + MCD^2 \cdot \sin^{-1}\left(\frac{0.5 \cdot SD}{MCD}\right)\right\}$	Adapted from Hughes (1998) and Jenkins and Keeley (2010)
Maximum capture distance (cm)	$MCD = \sqrt{\left[(RD)^2 - \left(V \cdot \frac{RD}{Vmax}\right)^2\right]}$	Hughes and Dill (1990)
Reactive distance (cm)	$RD = 12 \cdot PL\left[1 - e^{(-0.2 \cdot FL)}\right]$	Hughes and Dill (1990)
Prey Mass (g)	$PM = 0.0064 \cdot PL^{2.788} \cdot 10^{-3}$	Benke et al. (1999)
Fish Weight (g)	$FW = 0.0224 \cdot FL^{2.8379}$	Adapted from Bishop (1967)
Maximum Sustainable Swimming Speed ($cm \cdot s^{-1}$)	$Vmax = 36.23 \cdot FL^{0.19}$	Jones et al. (1974)

4.7. INPUT VARIABLES

Input variables for the model are velocity ($cm \cdot s^{-1}$), depth, and invertebrate drift concentration (number of $prey \cdot m^{-3}$; Table 4.3). Velocity affects both the swimming costs and encounter rate of invertebrates and is therefore an important factor in determining the net energy intake or habitat quality. Water depth plays a factor in the size of the area that Arctic grayling have for encountering prey. The amount of invertebrates also directly impacts the habitat quality via the availability of food for Arctic grayling.

Assumption:

- Prey density remains constant, regardless of the Arctic grayling density.
- Temperature will have a minimal effect on swimming costs and will not be included.

Table 4.3. Variables required for the Arctic grayling bioenergetics model to estimate habitat quality.

Input Variables	Parameter
Velocity ($cm \cdot s^{-1}$)	V
Stream Depth (cm)	SD
Prey Density (number of $prey \cdot m^{-3}$)	PD

4.8. OUTPUT

The Arctic grayling bioenergetics model can be used to determine stream habitat quality based on the model output. The model output of NEI does not give much context to the estimated quality of the stream habitat, other than negative NEIs are uninhabitable and positive NEIs are habitable. Also, by using NEI as the model output it would be difficult to validate the model directly by determining wild fish NEI. Instead, NEI can be converted into growth rates, which can be measured in wild fish. NEI can be converted into growth ($g \cdot day^{-1}$) by the estimated energy density of Arctic grayling:

(Eq. 16) $$Growth = NEI/(ED \cdot 24)$$

where ED is Energy Density ($J \cdot g^{-1}$) and 24 is to convert hours to days. Hayes et al. (2000) estimated the energy density of brown trout (*Salmo trutta*), a drift-foraging salmonid, using the following equation which will be utilized for Arctic grayling.

(Eq. 17) $$ED = 3148 \cdot e^{0.332 \cdot \left(100 \cdot \frac{FW}{FL^3}\right)} \cdot FW^{0.072}$$

Thus, the final output that will be used for the Arctic grayling bioenergetics model is growth.

Other than determining overall stream habitat quality, running simulations of the bioenergetics model can determine the optimal velocity and depth for Arctic grayling at the three life stages, and more importantly determine the minimum prey density required to support Arctic grayling in the stream (something that habitat suitability indices cannot determine).

4.9. DRAWBACKS

Aspects of the bioenergetics model can still be improved and some of the current weaknesses of the model are discussed below.

- The model is specific to drift-foraging Arctic grayling to determine stream habitat quality. This would not apply to conditions and behaviours in which Arctic grayling are not foraging such as migration, spawning or overwintering in lakes. The bioenergetics model would not be able to determine whether streams are passable for migrating or high quality spawning habitat.
- In the model, prey encounter rate depends on the water velocity of the stream. Therefore, at velocities of 0 $cm \cdot s^{-1}$ the model calculates prey availability as zero. In reality, food would be available in these stagnant areas. This could potentially be incorporated into the model later but at the moment the bioenergetics model focuses on drift-foraging Arctic grayling.
- Currently, the model does not have fish reach a level of satiation (i.e., maximum consumption per day), which can occur when food is abundant. Incorporating maximum consumption into the model would improve model accuracy in terms of realistic caloric intake.

- Including water temperature may also improve model accuracy, as was done with the HSI. Water temperatures can affect both behaviour and metabolic processes; the bioenergetics model incorporates the latter.
- By using equations for other fish species and various assumptions associated with the model components, the accuracy of the model output to realistic conditions is unknown.
- The ability of the model to function at multiple scales (e.g., microhabitat and whole stream scales) and accuracy among streams is also unknown.

5. DISCUSSION

5.1. HABITAT SUITABILITY INDEX MODELS

With the popularity of using HSI models, there are surprisingly few models that are validated (Hubert and Rahel 1989; Maughan and Barrett 1992; Roloff and Kernohan 1999; Haxton et al. 2008). Essentially, validating HSI models involves comparing population or fitness data, an inference to habitat quality, to values obtained from the HSI model. Typically it is abundance measures, such as density, that are compared to model outputs in validation studies. There are numerous steps involved with properly validating habitat suitability models to ensure their reliability (Roloff and Kernohan, 1999). Specifically, Roloff and Kernohan (1999) suggested the following to improve model reliability: calibrating the model, using a scale that incorporates the entire home range or life requisites, using an adequate sample size, sample over an adequate duration, compare models to fitness surrogates instead of abundance measures, and using statistics to objectively test the model.

Calibrating the model determines whether the model is sensitive enough to detect a difference between optimal and uninhabitable areas (Brooks 1997). The model needs adjustment if it is not sensitive to different habitat qualities. Thus, the model should be tested on areas that incorporate a spectrum of known habitat quality. If HSI scores fall within 0.3-0.7 the model cannot discern quality between sites adequately and calibration is required by adjusting the method of calculating the composite HSI (Brooks 1997). To calibrate the model, only habitat data is required.

An effective habitat suitability model should be at an appropriate scale that incorporates the species entire home range as well as entire life cycle. Given that Arctic grayling are migratory, this is difficult to incorporate. At the stream scale, adding an additional variable such as barriers to movement (e.g., culverts, dams, etc.) can aid with this. Also, "potential overwintering areas within a certain distance of the study stream" may be another variable to include. Regardless, it is important to remember that habitats are suitable if the entire life cycle can be carried out within the relative area.

Having an adequate sample size will depend on the scale of the study as well as what is considered an independent sample. If analyzing within a stream, then each unit area is a sample. If comparing between streams than each stream site is a sample. Regardless, an adequate sample size is required, more specifically in terms of sites occupied with fish. Having an adequate sample size will be both more difficult when comparing streams and dictated by logistics.

Ideally, it is best to measure population data over a few years to tease out temporal effects (Van Horne 1983). However, sampling over multiple years may not always be feasible and the variability in population data can potentially be accounted for by having a large sample sizes (i.e., streams).

Roloff and Kernohan (1999) suggested using fitness surrogates as opposed to abundance to infer habitat quality. It is commonly assumed that abundance is correlated to habitat quality. This assumption is important to consider as it is easy to measure abundance (e.g., presence, density) and employ in HSIs. It has been extensively argued, however, that density does not always correlate with habitat quality (Van Horne 1983; Roloff and Kernohan 1999; Railsback et al. 2003). Instead, fitness surrogates (e.g., reproductive success, growth, mortality rates) should better dictate habitat quality. However, fitness surrogates associated with specific habitats are much more difficult to estimate than abundance (Rosenfeld and Hatfield 2006). Thus, there is a trade-off between ease of obtaining data and accuracy of the data to indicate habitat quality. Regardless, the assumption that abundance or fitness surrogates indicate habitat quality is made by every HSI.

Instead of using density, other measures may be more suitable for predicting habitat quality. Biomass may be an effective way of measuring abundance as it takes into consideration that individuals vary in size. For instance, one large organism may occupy one area, whereas an area of similar quality could be occupied by two smaller organisms. Density indicates one area is of less quality, yet, the overall biomass shows the two areas are similar. Hubert and Rahel (1989) found that fish biomass did correlate with habitat variables, albeit not from typical velocity, depth, and substrate measures. Additionally, by measuring over a season, the change in biomass (e.g., growth) can be determined. Growth being a surrogate of fitness may be a better measure to compare to HSI values. Deegan and Peterson (1992) noticed an increase in growth via length and weight of Arctic grayling in fertilized (enhanced habitat) compared to non-fertilized habitat, while body condition, another surrogate of fitness, did not change. Jones et al. (2003a) found a similar trend regarding growth and body condition with Arctic grayling in natural versus artificial streams. Thus, to best acknowledge that abundance may not correlate with habitat quality, both, measures of biomass and growth, are recommended to validate HSI models.

5.2. BIOENERGETICS MODEL

Many assumptions go into the development of the bioenergetics models as well as relying on estimation of constants and using physiological and metabolic equations that may be inaccurate or intended for other species. As such there can be a high degree of error with the model output (de Kerckhove et al. 2008). Despite all the potential areas for model error, bioenergetics models are rarely validated (Ney 1993). Thus, it is important to ensure that bioenergetics models can also correctly rank habitat quality.

The validation method is similar to the method used for HSI, in which the model is tested by inputting parameter values measured in field studies and comparing the output of the model with the field observations (e.g., growth, density) (de Kerckhove et al. 2008). Field validation studies have been avoided due to the difficulty of getting accurate estimates of growth and consumption for fish (Ney 1993). Instead, sensitivity analyses are more likely to be performed, which determines how artificially changing input variables one at a time affects the output and whether the relative importance of the input variables are justified in accordance with natural systems (de Kerckhove et al. 2008). However, studies have been successful at incorporating field validations

into their models to determine if bioenergetics models properly assess habitat quality (e.g., Jones et al. 2003a; Rosenfeld et al. 2005), which greatly contributes to model reliability and the increasing popularity of their use.

The same and most important assumption also applies to validating the bioenergetics model in that population abundance or fitness surrogates may not necessarily correlate with the model output. Being aware of such assumptions will help in the improvement of the models predictive power.

6. SUMMARY

Two types of habitat models, HSI and bioenergetics model, were developed for Arctic grayling with specific focus on their northern distribution, which primarily occurs in Canada. Previously, Hubert et al. (1985) created an HSI for Arctic grayling, however, it included information from various stocked populations (e.g., Montana) and additional data has been gathered since the mid 80's. The HSI provided here includes the most recent habitat data on Arctic grayling and avoided information from stocked populations and other grayling species (i.e., European grayling). As such the HSI should be more accurate, specifically for Canadian populations, than the HSI provided by Hubert et al. (1985), however, validation in the field is recommended prior to use.

The bioenergetics model created for Arctic grayling was an amalgamation of information and equations from various sources. Previous bioenergetics models have been developed for Arctic grayling to determine stream position choice (e.g., Hughes and Dill 1990, Hughes 1998), however, this is the first bioenergetics model that specifically focuses on determining overall habitat suitability for Arctic grayling. Due to the heavy reliance on physiological and metabolic information and making numerous assumptions there is sometimes a high degree of error associated with the models output (de Kerckhove et al. 2008). Thus, it is also important that the Arctic grayling bioenergetics model be validated prior to use.

Model validation is an important step that should become mandatory in the process of making habitat models. The majority of habitat models are not validated and the accuracy of the models at predicting habitat quality is largely unknown (Ney 1993; Brooks 1997). Not only does model

validation determine model accuracy but also whether models are transferable to other locations. If habitat models are transferable between locations, it would greatly reduce the time and effort involved with creating location specific habitat models, and as a result, decision-making processes in habitat management would become more efficient. To validate a model, various aspects need to be considered (e.g., sensitivity to varying habitat qualities). Thus, the provided standardized validation protocol will make it easier to incorporate model validation into the habitat model making process as well as indicate the degree of confidence that habitat models can adequately indicate habitat quality.

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